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Species Characteristics

Coho salmon, as noted by Moyle (1976), Laufle et al. (1986), and Anderson (1995) are medium to large salmon, with spawning adults typically 40 to 70 cm (15.8 to 27.6 inches) fork length (FL) and weighing 3 to 6 kg (6.6 to 13.2 lbs). Coho salmon as large as 80 cm (31.5 inches) and 10 kg (22 lbs) have been caught in California. Identifying fin characteristics are 9 to 12 major dorsal fin rays, 12 to 17 anal fin rays, 13 to 16 pectoral fin rays, 9 to 11 pelvic fin rays (with an obvious axillary process at the fin base), a small fleshy adipose fin, and a slightly indented caudal fin. The scales are small and cycloid. The lateral line is complete and almost straight with 121 to 148 pored scales. Pyloric caeca number 45 to 83. There are 11 to 15 branchiostegal rays on either side of the jaw. Gill rakers are rough and widely spaced, with 12 to 16 on the lower limb (half) and 6 to 9 an the upper limb (half) of the first gill arch.

Spawning adults are generally dark and drab. The head and back are dark, dirty blue-green; the sides are a dull maroon to brown with a bright red lateral streak; and the belly is gray to black (Moyle 1976; Laufle et al. 1986; Sandercock 1991)). Females are paler than males, usually lacking the red streak. Characteristics of spawning males also include: hooked jaw, enlarged and more exposed teeth, slightly humped back and a more compressed head and body. The snout is less deformed than in other salmon species. Both sexes have small black spots on the back, dorsal fin, and upper lobe of the caudal fin. Except for the caudal and dorsal, the other fins lack spots. The gums of the lower jaw are grey, except the upper area at the base of the teeth, which is generally whitish.

Adult coho salmon in the ocean are steel-blue to slightly greenish on the back, silvery on the sides, and white on the belly. They have numerous small, irregular black spots on the back, upper sides above the lateral line, and base of the dorsal fin and upper lobe of the caudal fin. The adults have black mouths with white gums at the base of the teeth in the lower jaw; this is the most reliable physical feature that distinguishes them from chinook salmon (*O. tshawytscha*).

Juvenile coho salmon in inland waters are blue-green on the back, with silvery sides. The parr have 8 to 12 parr marks centered along the lateral line, which are more narrow than the pale interspace between them. The adipose fin is uniformly pigmented, or finely speckled giving it a grey or dusky color. The other fins lack spots and are usually orange tinted; however, the intensity of the orange tint varies greatly. The anal fin is pigmented between the rays, often producing a black and orange banding pattern. The anal fin is large, with the first few anterior rays elongated and white with black behind. The large eye and the characteristic sickle-shape of the anal and dorsal fins are characteristic of coho salmon juveniles that distinguishes them from juveniles of other Pacific salmon species.

Range

The coho salmon is one of seven species of Pacific salmon belonging to the genus *Oncorhynchus*, and one of two native salmon species regularly occurring in California. It occurs naturally in the north Pacific Ocean and tributary drainages. It ranges in freshwater drainages from Hokkaido, Japan and eastern Russian, around the Bering Sea and Aleutian Islands to mainland Alaska, and south along the North American coast to Monterey Bay, California (Figure 1).
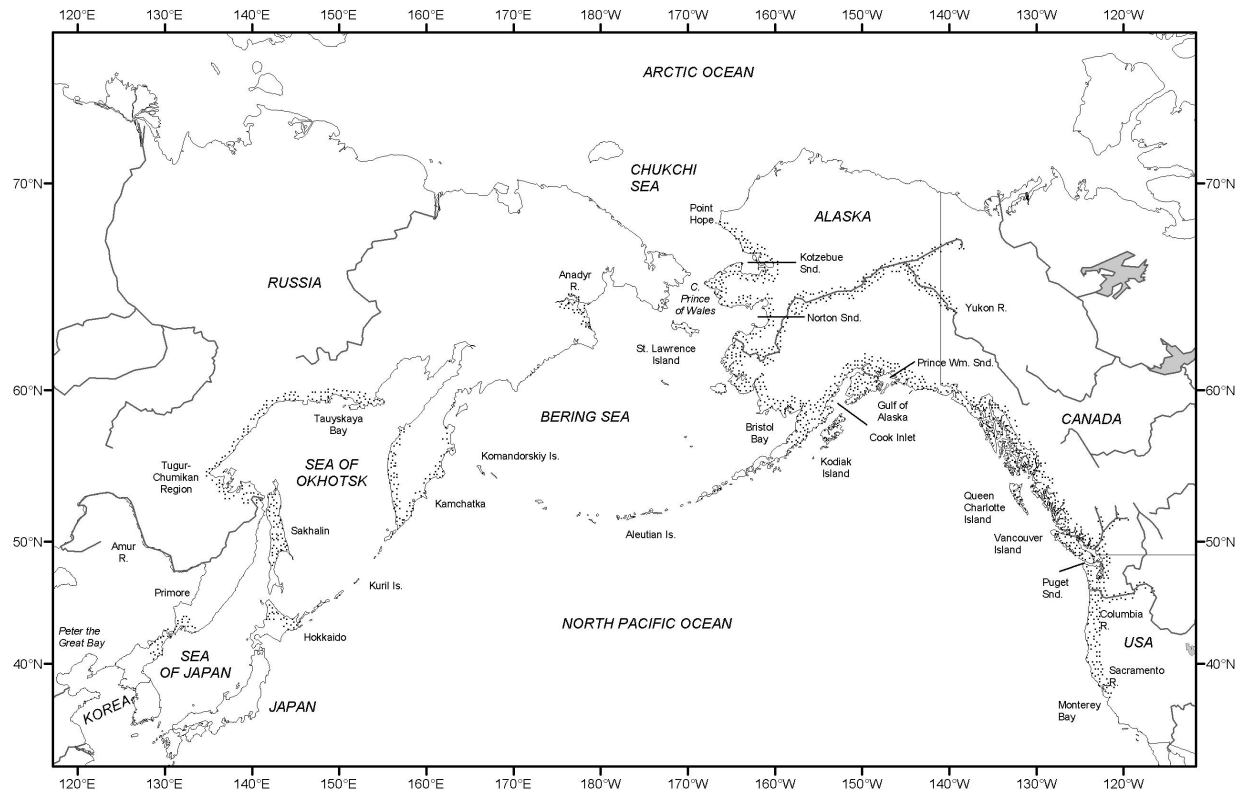
Figure 1. Native range of coho salmon (after Sandercock 1991).

Coho salmon historically ranged from the Oregon/California border (including the Winchuck and Illinois river drainages) south to the streams of the northern Monterey Bay (Snyder 1931; Fry 1973) including small tributaries to San Francisco Bay (Brown and Moyle 1991, Leidy and Becker 2001) (Figure 2). However, there is some evidence that they historically ranged as far south as the Pajaro River (Anderson 1995), the Big Sur River (Hassler et al. 1991), or even the Santa Ynez River (Lucoff 1980, as cited in National Council on Gene Resources 1982), although evidence of spawning populations south of the Pajaro River is anecdotal (Anderson 1995). Currently, the southernmost stream that contains coho salmon is Aptos Creek in Santa Cruz County (NMFS 2001a). Present distribution is shown in Figure 3.

Information on coho salmon in the San Joaquin and Sacramento rivers is sparse. Fry (1973) states that coho salmon did not occur in the Sacramento/San Joaquin river system prior to attempts to introduce them beginning in 1956. Hatchery fish returned in large numbers and spawned naturally, but were unable to maintain a natural run. Moyle (1976) notes that coho salmon in the Sacramento River are rare. It is likely that coho salmon historically observed in these streams were occasional strays (Hallock and Fry 1967; Hopkirk 1973). Intensive sampling efforts (trawling and beach seining) by the United States Fish and Wildlife Service (USFWS) in the Sacramento and San Joaquin rivers and estuary have recorded no coho salmon caught since the project began in 1976 (USFWS 2001 unpublished data). For these reasons, the Department does not consider the Sacramento/San Joaquin river system to be within the historical range of coho salmon.

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Figure 2. Historical distribution of coho salmon in California
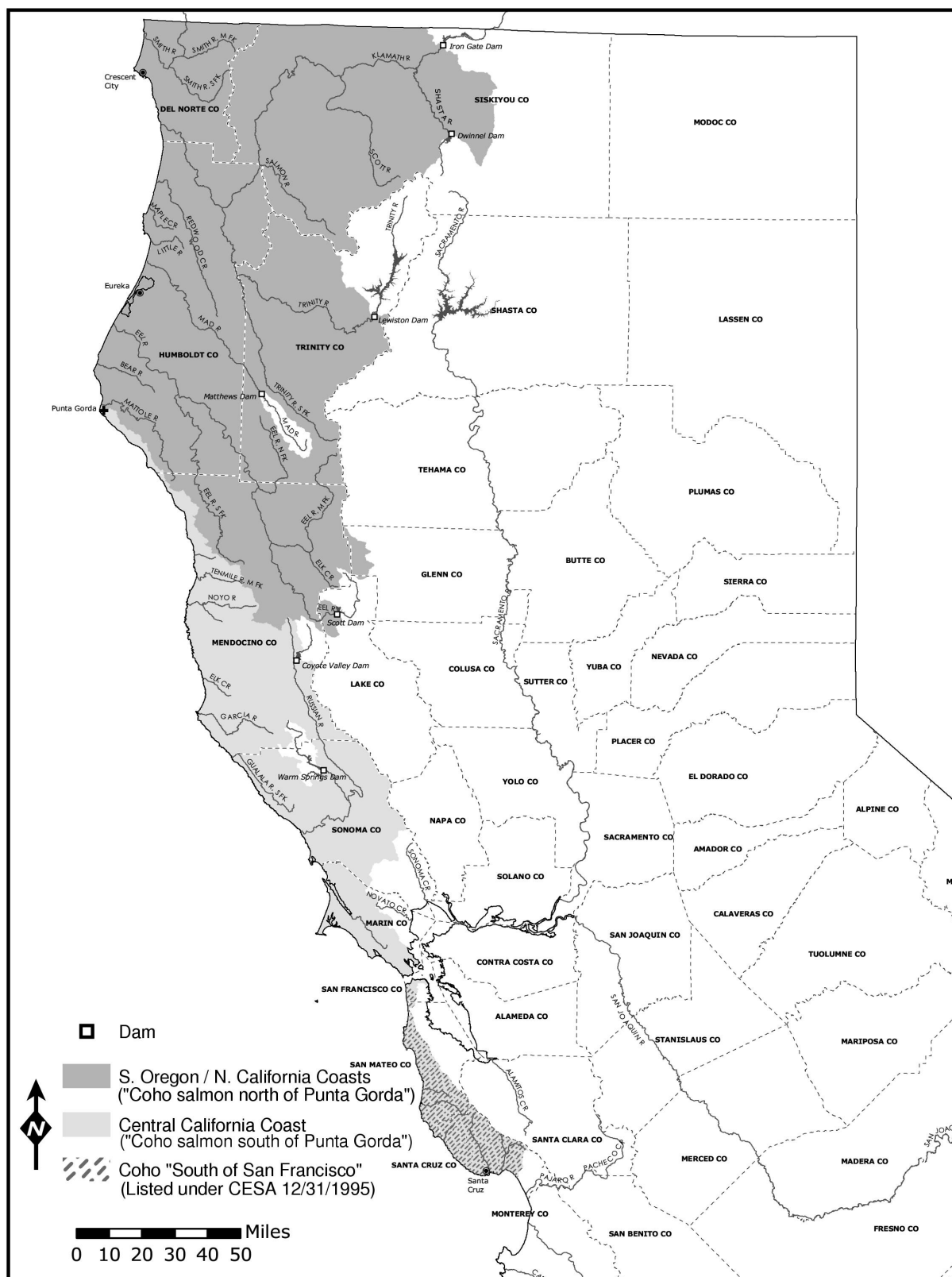
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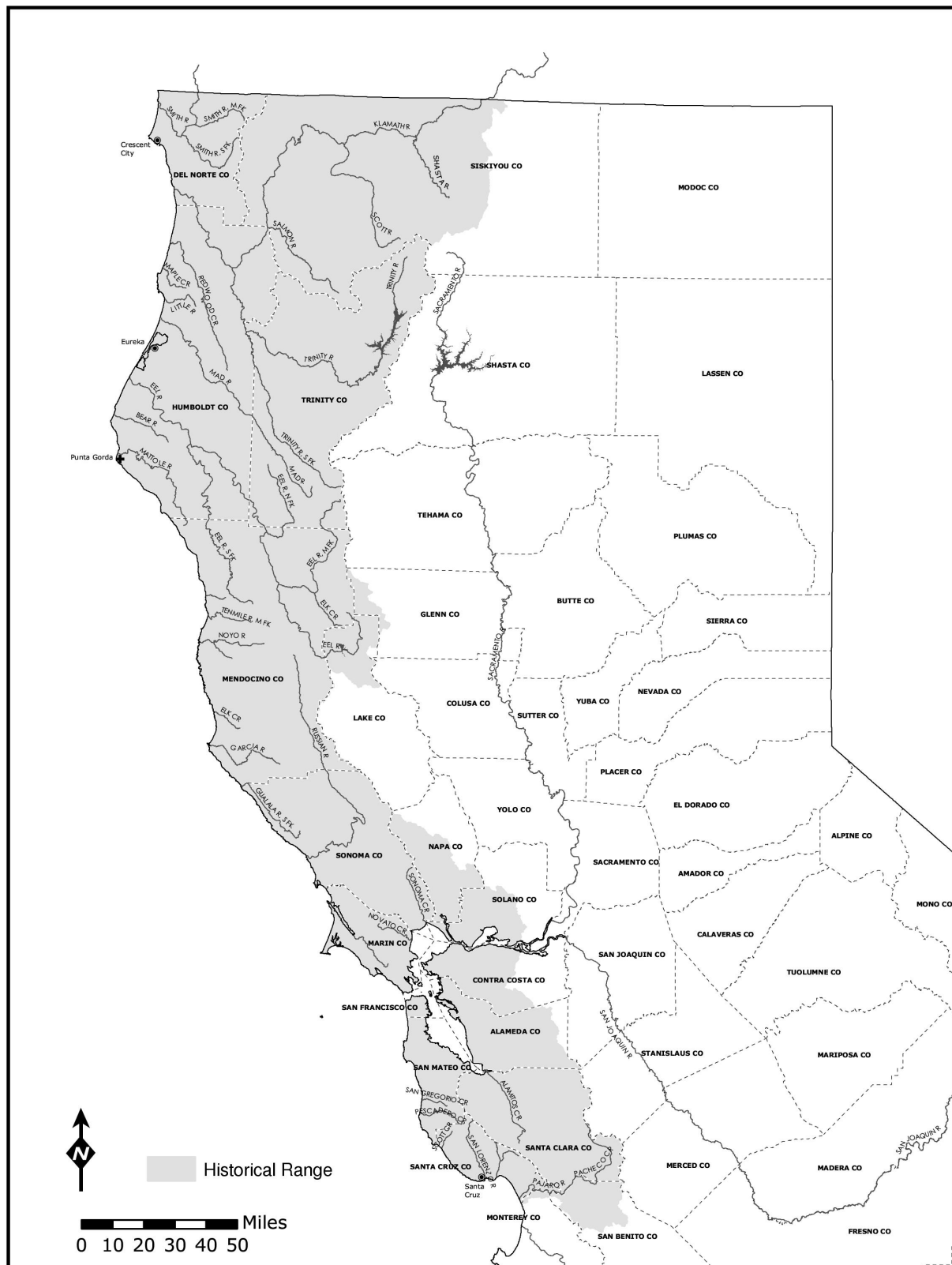
Figure 3. Present distribution of coho salmon in California. Shading depicts the general range of coho salmon. Coho salmon may not be present in all streams within the shaded area.

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Taxonomy and Systematics

Coho salmon belong to the class Osteichthyes (bony fishes), of the order Salmoniformes (salmon-like fishes), and are a member of the family Salmonidae (salmon, trout, and char). Walbaum (1792) originally described coho salmon on the basis of type specimens from rivers and lakes in Kamchatka, Russia. Table 1 shows the nomenclature for the species. The currently valid scientific name derives from a combination of Greek roots, *onkos* (hooked) and *rynchos* (nose), and *kisutch*, a colloquial name for the species in Kamchatka and Alaska (Hart 1973). The current English common name, coho, may have been used as early as 1878, when it appears as *co-hue*, a possible corruption of the similar Native American dialect names *kwahwult* (Chilliwack and Musqueam) and *kuchuks* (Sooke and Saanich)(Hart 1973, based on personal communication with Ricker).

Coho salmon are also known locally by the common names silver salmon, sea trout, saumon coho, and blueback (Scott and Crossman 1973). They are most commonly known in California as coho or silver salmon.

The systematic relationships of the five North American salmon in the genus *Oncorhynchus* have been described on the basis of morphology (Stearley 1992), allozyme variation (Utter et al. 1973), mitochondrial DNA (Thomas et al. 1986; Thomas and Beckenbach 1989; Shedlock et al. 1992; Domanico and Phillips 1995; Domanico et al. 1997), short interspersed repetitive elements (Murata et al. 1993, 1996), ribosomal DNA restriction fragment length polymorphisms (Phillips et al. 1992), nucleotide sequence of the D intron of growth hormone 2 (McKay et al. 1996), and nuclear DNA sequence data (Domanico et al. 1997). The general consensus of theses studies is that the Asian masu salmon (*O. masou*) is intermediate between rainbow trout (*O. mykiss*) and other Pacific salmon, and that the remaining *Oncorhynchus* species are arranged in two groups: one containing pink (*O. gorbuscha*) , sockeye (*O. nerka*), and chum (*O. keta*) salmon, and the other containing chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon. Although different studies support different relationships among the group containing pink, sockeye, and chum salmon, the group containing chinook and coho salmon is consistent. Based on these studies it is fair to state that coho salmon is most closely related to chinook salmon, and that the other three salmon species are more distantly related to them than they are to one another. Figure 4 shows a representative tree depicting the relationship among the North American *Oncorhynchus* species.

Table 1. Nomenclature for coho salmon (after Scott and Crossman 1973).

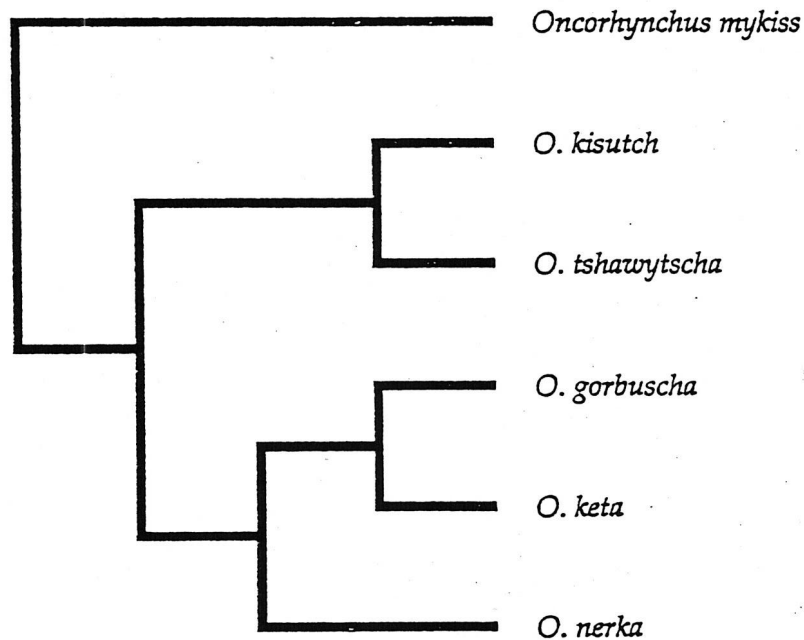| Scientific name	Authority
Salmo kisutch	Walbaum 1792: 70 (type locality rivers and lakes of Kamchatka, Russia)
Salmo tsuppitch	Richardson 1836: 224
Oncorhynchus kisutch (Walbaum)	Jordan and Evermann 1896-1900: 480

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Figure 4. Bootstrapped parsimony tree showing the relationship of the six North American *Oncorhynchus* species that represent Pacific salmon using combined nuclear and mitochondrial DNA data. (After Domanico et al. 1997, with modification)

Genetics

Coho salmon population genetic structure has been studied using allozyme[3], transferrin[4], and DNA data since 1982 (Weitkamp et al. 1995). Most of these studies largely concern areas outside California. For example, Olin (1984) and Hjort and Schreck (1982) focus on more northerly populations and only include one or a few samples from California for comparison. Only a few published studies concentrate exclusively on relationships within and among California populations. In addition Weitkamp et al. (1995) caution that studies prior to 1988 may be limited by their inclusion of less than half of the ten most polymorphic allozyme loci[5] for coho salmon (Milner 1993). Also, studies including data from the transferrin locus are likely biased by selection acting on the transferrin gene (Weitkamp et al. 1995, Ford et al. 1999). A few of the other studies mentioned here (Banks et al. 1999, Hedgecock 2001) are not peer reviewed. Sample locations for genetic studies reviewed in this section are shown in Table 2.

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[3] Alternate forms of an enzyme produced by different alleles and often detectable by electrophoresis.

[4] A polymorphic iron-binding protein found in body fluids that is important in iron metabolism and resistance to bacterial infection.

[5] Locus (pl. loci): the location of a gene on a chromosome. *Polymorphic loci* are those that have more than one allele.

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Table 2. Sample locations for genetics studies reviewed in the text.

Literature Source	Sample Locations
Bartley et al. 1992	**California**: Scott Creek, Waddell Creek, Lagunitas Creek, Tanner Creek/Salmon Creek, Willow Creek/Russian River, Flynn Creek/Navarro River, John Smith Creek/Navarro River, Albion River, Little River, Twolog Creek/Big River, Russian Gulch, Caspar Creek, Hare Creek, Little North Fork Noyo River, Kass Creek/Noyo River, Pudding Creek, Little North Fork Ten Mile River, Cotteneva Creek, Huckleberry Creek/South Fork Eel River, Butler Creek/South Fork Eel River, Redwood Creek/South Fork Eel River, Elk River, Prairie Creek, Rush Creek/Trinity River, Trinity River Hatchery, Deadwood Creek/Trinity River, West Branch Mill Creek/Smith River
Hjort and Schreck 1982	**Washington**: Quilcene River, Quinault River **Oregon**: Cascade Hatchery/Columbia River, Beaver Creek, Cowlitz Hatchery stock (Cascade Hatchery), Sandy River Hatchery/Columbia River, North Nehalem River Hatchery, Trask River Hatchery, Salmon River Hatchery, Fall Creek Hatchery/Alsea River, Umpqua Hatchery stock/Smith River (Cole Rivers Hatchery), Rogue River **California:** Iron Gate Hatchery/Klamath River, Trinity River Hatchery, Mad River Hatchery
Olin 1984	Oregon Coast (23 samples) and Iron Gate Hatchery, California (1 sample)
Solazzi 1986	Data source was combination of the same data reported in Olin 1984 and Bartley et al. 1992.
Weitkamp et al. 1995	**Alaska:** Cabin, Kartam, Campbell, Goodnews **British Columbia:** Chilliwack, Coldwater, Cowichan, Big Qualicum, Roberson, Capilano, Squamish **Washington**: Lewis and Clark, Grays, Big Creek, Clatskanie, Cowlitz, Scappoose, Lewis, Clackamas, Eagle, Sandy, Hardy, Bonneville, Willard, Naselle, Nemah, Willapa, Chehalis, Humptulips, Queets, Quillayute, Soleduck, Hoko, Hood Canal, Big Beef, Green, Snohomish, Stillaguamish, Skagit, Nooksack **Oregon**: Rogue, Elk, Sixes, New, Coquille, Coos, Eel, Tenmile, Umpqua, Smith, Tahkenitch, Alsea, Beaver, Siletz, Salmon, Trask, Nehalem **California**: Scott Creek, Lagunitas Creek, Tanner Creek/Salmon Creek, Russian River/Willow Creek, Navarro River/Flynn Creek/John Smith Creek, Albion River, Little River, Russian Gulch, Caspar Creek, Hare Creek, Pudding Creek, Cottoneva Creek, Huckleberry Creek/South Fork Eel River, Butler Creek/South Fork Eel River, Redwood Creek/South Fork Eel River, Elk River, Deadwood Creek/Trinity River, Trinity River Hatchery, Iron Gate Hatchery/Klamath River, West Branch Mill Creek/Smith River
Banks et al. 1999	**California**: Warm Springs Hatchery/Russian River, Green Valley Creek/Russian River, Olema Creek, Noyo Egg Taking Station/Noyo River, Hare Creek
Hedgecock 2001	**California**: Eel River, Noyo River, Russian River, Lagunitas Creek, Olema Creek, Scott Creek

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In the most comprehensive study of California coho salmon population genetics, Bartley et al. (1992) studied variation in 22 allozyme loci in 27 populations. The authors stated that the study could be improved by increasing sample sizes; average sample size in this study was 34 fish. The study reported low levels of variability and little evidence of geographic pattern in the observed variation. There were significant allele frequency[6] differences among samples and within six regional groupings. Average gene flow between populations in this study was estimated from genetics data to be 1.3 fish per generation.

Hjort and Schreck (1982) looked at population structure using a method based on frequencies for one allozyme locus and the transferrin locus. They also included life history and morphological characteristics in their study. Of the 35 sample locations examined in this study, only three were from California. Most samples were from Oregon (23) with some from Washington. Cluster analysis led to identification of three major groupings: 1) North Coast Oregon hatcheries, 2) Columbia, Rogue and Klamath rivers, and 3) Coastal Oregon samples. Several populations were outliers, including one sample from the Mad River Hatchery in California. These outlier populations were distinct from one another and other groups.

Olin (1984) studied population structure in Oregon coho salmon populations. This study also included one sample from the Iron Gate Hatchery (Klamath River) in California. Variation was observed at 31 of the 53 loci examined. The study found a low level of genetic variability. In this study, the Klamath River sample clustered with those from the Rogue River in a southerly cluster that was most genetically distinct from more northerly groupings, two of which overlapped geographically and were similar genetically. The similarity of the Iron Gate Hatchery sample and Rogue River groups was attributed by the author to geographic proximity, straying, and unrecorded egg transfers.

Solazzi (1986) inspected a dendrogram[7] based on allozyme and transferrin data contained in Olin (1984) and Bartley et al. (1992). The dendrogram included eight samples from the Columbia River, 28 from the Oregon coast, and 16 from the California coast. Three major clusters were discernable: 1) Oregon coast north of the Rogue River, 2) Columbia, Rogue and Klamath rivers plus two samples from two rivers north of Cape Mendocino, and 3) California samples from south of Cape Mendocino. Eight other samples from the Oregon coast and California were outliers to the major clusters.

NMFS (Weitkamp et al. 1995) developed new data and reanalyzed combined data in a review of the status of coho salmon pursuant to ESA listing. Allozyme data were collected from coho salmon populations across their North American range. However, the new data study focused on populations from Oregon, Washington, British Columbia, and Alaska. Only one new sample from California (Trinity River Hatchery, 1982, N = 98) was included in the new data analysis. Eighty-seven allozyme loci were examined. In a dendrogram of genetic distance[8] measures (Cavalli-Sforza and Edwards 1967), the California sample clustered with samples from the Rogue, Elk, and Umpqua rivers in Oregon.

Because the new data set only contained a single California sample, NMFS (Weitkamp et al. 1995) also conducted a reanalysis of combined data for Oregon and California. Data from

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[6] Allele: a variant form of a gene. *Allele frequency* is the proportion of all of the alleles in a population that is of one type.
[7] A branching diagram that provides a way of visualizing similarities among different groups or samples.
[8] A quantitative measure of genetic differences between a pair of samples.

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Olin (1984) and Bartley et al. (1992) were combined with the new data for reanalysis. Because the data are not directly comparable, genetic distance calculations (Cavalli-Sforza and Edwards 1967) were made using the maximum number of alleles in common between each pair of populations being compared. Two major geographic clusters, separated by a relatively large genetic distance, were identified: 1) a northern, mostly large rivers cluster containing samples from the Elk River, Oregon, to just north of Cape Mendocino, including the Eel River; and 2) a more southerly, mostly small rivers group, containing nine samples from Fort Bragg to Lagunitas Creek, and three samples from north of Cape Mendocino. Samples from Scott, Cotteneva, and Pudding creeks (Santa Cruz, Mendocino, and Mendocino counties respectively) were outliers to both major clusters. NMFS found considerable genetic diversity within each of the major groupings.

Data summarized in the NMFS status review of coho salmon (Weitkamp et al. 1995) were used to document areas of "genetic discontinuity/transition" for delineation of ESU boundaries. These discontinuities represent areas of restricted gene flow that likely results in some level of reproductive isolation. In California, this area of discontinuity occurs around Punta Gorda, i.e., populations north and south of Punta Gorda likely experience some level of gene flow restriction that is greater than that experienced within each geographic region. NMFS identified two ESUs that encompass California coho salmon populations: 1) the CCC Coho ESU from Punta Gorda south to the San Lorenzo River (the southernmost natural population of coho salmon in California); and 2) the SONCC Coho ESU extending from Punta Gorda north to Cape Blanco, Oregon. Populations in the transition region around Punta Gorda are not easily placed in either north-south geographic region. NMFS identified four other more northerly ESUs that extend from Oregon to Alaska.

Recent data in unpublished, non peer-reviewed reports include Banks et al. 1999, which reports on limited microsatellite data from the California coast. The authors stress that these results are preliminary, based on small samples containing a large proportion of juveniles from a small number of sampling events, with only a few loci included in the analysis. Samples included hatchery origin adults from Warm Springs Hatchery (Russian River, 1992 and 1993), juveniles from Green Valley Creek (Russian River, 1997 and 1998), juveniles from Olema Creek (1997), adults from Noyo Egg Taking Station (1994), and juveniles from Hare Creek (1997). Tests for homogeneity (i.e., uniformity) among populations based on data from five microsatellite loci indicated substantial genetic heterogeneity such that only a few of the samples could be pooled for analysis. The authors stated that this heterogeneity suggests that genetic drift might strongly influence these populations. A neighbor-joining phenogram of Nei's genetic distance (Nei 1972) constructed using data from two microsatellite loci yielded the following tentative relationships:

- Warm Springs Hatchery 1996 and 1997 (Brood year 1993) and Olema Creek samples clustered together;
- samples from Noyo Egg Taking Station and Hare Creek appear to be closely related;
- samples from Green Valley Creek collected in 1997 were combined with the 1995-1996 (Brood year 1992) Warm Springs Hatchery sample, suggesting that this year class is strongly influenced by the hatchery stock; and
- separate clustering of the 1998 Green Valley Creek sample suggests that they may represent remnants of a "more wild stock".

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Hedgecock (2001) reported on analysis of a limited number of samples from seven populations of California coho salmon (Eel, and Russian rivers, Noyo Egg Taking Station, Lagunitas, Olema, and Scott creeks). Several of these populations, including some consisting of adults, failed to meet random mating expectations. Although data are limited and conclusions from them should be viewed with caution, one possible explanation is that some of the coho salmon populations in this analysis are already experiencing the effects of inbreeding (Hedgecock 2001). Genetic distances among sites are in general agreement with currently defined ESU structure (Weitkamp et al. 1995). Samples from sites within the CCC Coho ESU North of San Francisco form a reasonable cluster, joined next by Scott Creek, and finally by the Eel River.

No recent comprehensive study of coho salmon population genetics covering the range of coho salmon in California is available. Some studies (Bartley et al. 1992, Olin 1984) found a generally low level of diversity in California coho salmon. The reason for this low diversity is not clear. It may be a result of current or historical reduction in population size of all or a large portion of the existing natural spawning populations, historical naturally low population sizes in all coho salmon populations, or some level of homogenization of stocks. Also, some of the existing studies may not have adequately captured the true range of genetic variation in coho salmon because of limited geographic context, availability of variable loci, small sample size coupled with low levels of variation in a large number of loci examined, and complications due to the effects of selection in transferrin studies (Weitkamp et al. 1995, Ford et al. 1999). Weitkamp et al. (1995) and preliminary data in Banks et al. (1999) found substantial genetic diversity in the samples that they analyzed. All of the studies that attempted it were able to discriminate groups of coho salmon. These relatively consistent patterns are summarized in the NMFS ESU delineations.

Historical stock transfers and outplanting may have obscured geographic patterns of genetic variation in California coho salmon (see Chapter VI, *Hatcheries* and Chapter VII, *Hatchery Operations*). Although the relationship of genetic structure to geography is weak, there is a fairly strong separation between clusters of coho salmon populations north and south of Punta Gorda that also correspond to different ecological features in the two areas. Populations south of San Francisco may be separable from other California stocks. However, extremely small stock sizes in this area and hatchery influence greatly complicate the analysis. More data are needed to properly evaluate this relationship.

Preliminary data suggest that inbreeding may already be occurring in the Russian River coho salmon populations. This is troubling because of the known deleterious effects of inbreeding on production and growth and their implications for recovery potential (see Chapter VI, *Hatcheries* and *Genetic Diversity*).

The Evolutionarily Significant Unit Concept As Applied to Endangered Species Act Pacific Salmon Listings

Under the federal ESA, the definition of species includes "any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature". In order to improve consistency, NMFS developed the ESU concept. In the document describing this concept, Waples (1991a) states, "A population (or group of populations) will be considered distinct (and hence a 'species') for purposes of the ESA if it represents an ESU of the biological species." A population must meet two criteria in order to be considered an ESU: 1) it must be reproductively isolated from other conspecific population units, and 2) it must represent an important component of the evolutionary legacy of the species (Waples 1991a).

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Genetic analyses can be especially useful for evaluating ESU criteria. Since the relationship between genetics and phenotypic and/or life history characters is generally unknown (Myers et al. 1998), NMFS often relies heavily on direct genetics data for evidence of reproductive isolation. However, other data, within their limitations, can and should be used to evaluate the reproductive isolation criterion when they are available.

Two ESUs of coho salmon are found in California; one is entirely within California's borders (Figure 5). They are the SONCC Coho ESU, from Punta Gorda, California, north across the state border to Cape Blanco, Oregon, and the CCC Coho ESU, from Punta Gorda, California, south to the San Lorenzo River, California. Both are listed as threatened under the ESA. Only naturally spawning populations within these ESUs were included in the federal listings. The Mad River Hatchery population was deemed not a part of the ESU. The relationship of the Iron Gate Hatchery stock with the rest of the SONCC Coho ESU was judged "uncertain", and was therefore not included as part of the ESU. Four other populations deemed "hatchery populations" (Mattole River, Eel River, Trinity River, and Rowdy Creek) were specifically included as part of the ESU, but none were deemed essential to recovery, and were therefore not included in the listing. Any hatchery population that is included as part of an ESU may have a role in its recovery under certain conditions. (Current hatchery production is described in Chapter VII "Hatchery Operations")

ESUs reflect the best current understanding of the likely boundaries of reproductively isolated salmon populations over a broad geographic area. Understanding these boundaries is especially important for NMFS, which is charged with evaluating and protecting salmon species with broad ranges extending across state borders. Similar populations can be grouped for efficient protection of bio- and genetic diversity. The Department, in contrast, has responsibility for evaluation and protection of California stocks only. Therefore, the Department typically evaluates and manages salmon on a watershed basis, regardless of the biological affinities of California stocks to stocks across our borders. The Department recognizes the importance of genetic structure and biodiversity among California stocks in evaluating and protecting coho salmon. For example, the genetic affinities among nearby coho salmon populations will be used as part of the information in choosing appropriate broodstock to assist in the recovery of Russian River coho salmon. The Department's status review also responds directly to the geographic range and stocks specified in the petition to list. In the present case, coho salmon north of San Francisco are specified in the listing petition. Therefore, the status review focuses on information for all populations, including hatchery populations in that area.

The coho salmon ESU delineations described in Weitkamp, et al. (1995) represent important information about likely relationships among, and reproductive isolation of, coho salmon populations in California waters and the extension of affinities across the Oregon border. This information has important implications for interstate coordination of management, ocean harvest management, recovery planning, and recovery-action implementation. This approach is consistent with previous listings, the federal approach to species' evaluation, and the generally accepted biological criterion that a species is "a group of interbreeding organisms that is reproductively isolated from other such groups" (Mayr 1966). The Department agrees with NMFS that the coho salmon ESU designations are valid and justifiable constructs, both from a biological and management perspective, and that they represent distinct population segments of coho salmon.

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Figure 5. Coho salmon Evolutionarily Significant Units (ESU) in California.

Life History and Unique Characteristics

Adult coho salmon in general enter fresh water to spawn from September through January (Figure 6). In the short coastal streams of California, migration usually begins mid-November through mid-January (Baker and Reynolds 1986). Coho salmon move upstream usually after heavy fall or winter rains have opened the sand bars that form at the mouths of many California coastal streams, but the fish can enter the larger rivers earlier. On the Klamath River, coho salmon begin entering in early- to mid-September and reach a peak in late September to early October. On the Eel River, coho salmon return four to six weeks later than on the Klamath River (Baker and Reynolds 1986). Arrival in the upper reaches of these streams generally peaks in November and December. Neave (1943), Brett and MacKinnon (1954) and Ellis (1962) indicate that coho salmon tend to move upstream primarily during daylight hours. They also state that diurnal timing varied by stream and/or flow, but the majority moved between sunrise and sunset.

Generally, coho salmon spawn in smaller streams than do chinook salmon. In California, spawning mainly occurs from November to January although it can extend into February or March if drought conditions are present (Shapovalov and Taft 1954) (Figure 6). In the Klamath and Eel rivers, spawning occurs November to December (USFWS 1979). Shapovalov and Taft (1954) noted that the females choose the spawning sites usually near the head of a riffle, just below a pool, where the water changes from a laminar to a turbulent flow and there is a medium to small gravel substrate. The female digs a nest (redd) by turning partly on her side and using powerful rapid movements of the tail to dislodge the gravels, which are transported a short distance downstream by the current. Repeating this action creates an oval to round depression at least as deep and long as the fish. Eggs and sperm (milt) are released into the redd, where, due to the hydrodynamics of the redd, they tend to remain until they are buried. Approximately 100 or more eggs are deposited in each redd. The fertilized eggs are buried by the female digging another redd just upstream. The flow characteristics of the redd location usually ensures good aeration of eggs and embryos, and flushing of waste products.

There is a positive correlation between fecundity of female coho salmon and body size, and there is a definite tendency for fecundity to increase from California to Alaska (Sandercock 1991). Average coho salmon fecundities, as determined by various researchers working on British Columbia, Washington, and Oregon streams, range from 1,983 to 2,699 and average 2,394 eggs per female Sandercock (1991). Scott and Crossman (1973) found that fecundity of coho salmon in Washington streams ranged from 1,440 to 5,700 eggs for females that were 44 to 72 cm in length.

In California, eggs incubate in the gravels from November through April (Figure 6). The incubation period is inversely related to water temperature, but the embryos usually hatch after eight to twelve weeks. California coho salmon eggs hatch in about 48 days at 48 $^{\circ}$F, and 38 days at 51.3 $^{\circ}$F (Shapovalov and Taft 1954).   After hatching, the alevins (hatchlings) are translucent in color (Shapovalov and Taft 1954, Laufle et al. 1986, Sandercock 1991). This is the coho salmon's most vulnerable life stage when they are susceptible to siltation, freezing, gravel scouring and shifting, desiccation, and predators (Sandercock 1991, Knutson and Naef 1997, PFMC 1999).   They remain in the interstices of the gravel for two to ten weeks until their yolk sac has absorbed (becoming pre-emergent fry), at which time their color changes to that more characteristic of fry (Shapovalov and Taft 1954, Laufle et al. 1986, Sandercock 1991). These

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color characteristics are silver to golden with large vertically oval parr marks along the lateral line that are narrower than the spaces between them.

The fry emerge from the gravel between March and July, with peak emergence occurring from March to May, depending on when the eggs were fertilized and the water temperature during development (Shapovalov and Taft 1954) (Figure 6). The fry seek out shallow water, usually moving to the stream margins, where they form schools. As the fish feed heavily and grow, the schools generally break up and the juveniles (parr) set up territories. As the parr continue to grow and expand their territories, they move progressively into deeper water, until July and August when they are in the deepest pools (CDFG 1994a). This is the period of maximum water temperatures, when growth slows (Shapovalov and Taft 1954). Food consumption and growth rate decrease during the months of highest flows and coldest temperatures (usually December to February). By March, following the resumption of peak flows, they again begin to feed heavily and grow rapidly.

Rearing areas generally used by juvenile coho salmon are low gradient coastal streams, wetlands, lakes, sloughs, side channels, estuaries, low gradient tributaries to large rivers, beaver ponds and large slackwaters (PFMC 1999). The more productive juvenile habitats are found in smaller streams with low-gradient alluvial channels containing abundant pools formed by large woody debris (LWD). Adequate winter rearing habitat is important to successful completion of coho salmon life history.

After one year in fresh water, the smolts begin migrating downstream to the ocean in late-March or early April. In some years emigration can begin prior to March (CDFG unpubl. data) and can persist into July in some years (Shapovalov and Taft 1954, Sandercock 1991). Weitkamp et al. (1995) indicates that peak downstream migration in California generally occurs from April to late May/early June (Figure 6). Factors that affect the onset of emigration include the size of the fish, flow conditions, water temperature, dissolved oxygen (DO) levels, day length, the availability of food. In Prairie Creek, Bell (2001) indicated there is a small percentage of coho salmon that remains more than one year before going to the ocean. Low stream productivity, due to low nutrient levels and or cold water temperatures, can contribute to slow growth, potentially causing coho salmon to reside for more than one year in fresh water (PFMC 1999). Though there may be other factors that contribute to a freshwater residency of longer than one year, Bell (2001) suggests that these fish are spawned late and are too small at time of smolting.

The amount of time coho salmon spend in estuarine environments is variable, though PFMC (1999) indicated the time spent is less in the southern portion of their range. Upon ocean entry the immature salmon remain in inshore waters, collecting in schools as they move north along the continental shelf (Shapovalov and Taft 1954; Anderson 1995). Most remain in the ocean for two years, however, some return to spawn after the first year, and these are referred to as grilse or jacks (Laufle et al. 1986). Data on where the California coho salmon move to in the ocean are sparse, but it is believed they scatter and join schools of coho salmon from Oregon and possibly Washington (Anderson 1995).

III. BIOLOGY

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Adult migration	▓									▓	■	■
Spawning	■	▓								▓	■	■
Egg Incubation	■	■	■	▓							▓	■
Emergence/ Fry		▓	■	■	■	▓						
Juvenile rearing	■	■	■	■	■	■	■	■	■	■	■	■
Out-Migration			▓	■	■	■	▓					

Figure 6. Generalized life stage periodicity of coho salmon in California Coastal watersheds. Gray shading represents months when the life stage is present, black shading indicates months of peak occurrence.